## XXII.—*Larval Theory of the Origin of Tissue.* By A. HYATT *.

I HAVE endeavoured, in the essay of which this is an abstract, to demonstrate a phyletic connexion between Protozoa and Metazoa, and also to show that the tissue-cells of the latter are similar to asexual larvæ and are related by their modes of development to the Protozoa, just as larval forms among the Metazoa themselves are related to the ancestral adults of the different groups to which they belong. This is indicated by the fact that the tissue-cells exhibit highly concentrated or accelerated modes of development according to a universal law of biogenesis, which has now been found in almost all groups of animals. Thus in forms which stand at the extreme limits of groups in point of specialization of structure, or have unusually protected young, or pathological forms with stimulated development—in fact any forms in which stimulative causes have acted upon the young, so as to bring about an earlier development at the expense of the normal rate of growth—there may be observed an abbreviation of the usual series of structural characters, which appear in the young of normal forms of the same group. The observations of many authors, notably Cope, Häckel, Balfour, Weissmann, Packard, and Wurtemburger, have conclusively proved that examples of abbreviated or concentrated development are the results of a constant tendency in all organisms to acquire characters in adults or later stages of larvæ, and then to inherit these at earlier and earlier stages in successive descendants; thus finally crowding the younger stages until some ancient characters are skipped, sometimes leaving no record of the derivation of the organism, and at others only a highly abbreviated record in the earlier stages.

No bushy colonies of zoöns or cells are built up in the Metazoa, representing the incompletely divided colonies of the adults of Protozoa, except in cases of incomplete segmentation of the ovum. These forms are skipped, and the complex colonies, which arise by fission, consist of zoöns divided by distinct walls. The cycle of transformations is not only shortened by this omission, but the origin of the reproductive bodies is carried back into the earlier stages in many forms,

* From the 'American Journal of Science' for May 1886, pp. 332–347. This article is an abstract of a paper with the same title published in Proc. Bost. Soc. Nat. Hist. vol. xxiii. 1884, pp. 45–163, but has in addition the suggestion that *Volvox* and *Eudorina* are true intermediate forms entitled to be called Mesozoa or Blastrea.

and the rapidity of the processes of complete fission, due to concentration, produces masses of tissue and membranes in place of loosely connected colonies, as among Protozoa *.

The many disconnected wandering cells, with their independent organization and functions, favour this conclusion, and the sight of these and of ova in the mesenchyme of sponges, and the evidence of their functions here and elsewhere in the animal kingdom, is sufficient to bring a candid mind to open confession of the existence of exact parallelism between them and the single individualized Amœba.

These and other morphological facts have led, so far as we know, only to comparisons between the ordinary tissue-cells and the adults of the Amœbæ, and it has been assumed that these cells are the equivalents of the adult Amœbæ.

Morphologically this seems to be true; but it does not account for the physiological differences between the Protozoon and the cell. The ontology of the cell, its production of tissue, and the reduction of the cycle of transformations cannot be explained unless we attribute to it a concentrated energy in reproduction and a tendency to form closely united and complex associations much greater than that of the Protozoon.

Thus a single Metazoon is a colony of infinite complexity in which the two primitive colonies, ectoderm and endoderm, have produced by growth and agamic fission all the anatomical systems and their various organs and smaller parts.

Studies of reproduction show that the succession of events among Protozoa was first growth, then fission, then the union or concrescence of divided zoöns and an exchange of their complementary parts; evidently all of these influences bear upon the tissue-cell and influence its reproduction. Nevertheless two cells do not combine previous to reproduction by fission, and whatever the effect of the original impregnation may be, we are obliged therefore to regard a young cell as a modified agamic larva-like form or zoön when compared with the full-grown Amœba. If descent from Amœbæ through Flagellata and Ciliata is assumed, then the task of proving young cells to be immature forms becomes easier. In this case they are obviously forms which, like the ova of many Metazoa, have retained their ancient amœboidal characteristics, while losing their later-acquired flagellate and ciliate similarities.

We cannot use the words embryo and larva, which belong

* The network of protoplasm connecting tissue-cells is disregarded in order to show the massive nature of tissues and at the same time state their characteristic cellular composition.

to the ovum after impregnation, and we therefore propose to designate the cell an autotemnon *, in contrast with the embryo, which is more specialized. The least specialized tissue-cells of the mesenchyme differ less from the individualized agamic zoöns of the Protozoa, while the spermatocysts, as more highly specialized encysted male zoöns, retain the cycle of agamic transformations derived from their male Protozoonal prototypes, and are intermediate to the encysted female zoön or ovum.

The spermatocyst, in other words, is not dependent upon impregnation for its development, and has necessarily retained more of the characteristic successive transformations of the primitive agamic forms than the ovum. This last has become dependent upon impregnation. The tendency to earlier and earlier impregnation in successive generations, and the correlative concentration of autotemnic stages, as shown by the fission of the nucleus and exclusion of the polar globules, has finally established the ovum as a more highly specialized form of cell.

The conditions of fission in the cyst of a Protozoon and in the ovum and spermatocyst are similar as long as the zoöns or cells are all similarly confined; but when they burst the envelope and become free the surrounding conditions differ, and they correspondingly diverge.

The early encystment of the ovum, the non-production of the colonial form by incomplete fission, the dependence of the feminonucleus upon impregnation, and the great rapidity and extensive character of the changes by which the diploblastic parenchymula and triploblastic gastrula are built up, all show the excessive concentration of development which has taken place, when any blastula is compared with the corresponding forms among the Volvocinæ. There is also a distinction between the mode of development of the Volvocinæ and the lower Protozoa, which has, we think, great significance. They have prolonged gestation, and this can be compared with the similar prolongation of the corresponding period in the early inception of the ovum in the Metazoa.

They are, however, necessarily only single cells. The whole process of segmentation occurs under conditions which effectually protect the earlier stages in the higher Protozoa and in all the Metazoa; but, as might have been anticipated, the more specialized Metazoon elaborates at once and within limits of this early egg stage a fully-formed colony, the blastula, whereas the highest and most specialized of Protozoa

* From αὐτὸς, self, and τέμνω, to divide.

get no further than the production of single ova and spermatocysts *, or the earliest stages of segmentation, during the same period. The adult condition of *Eudorina* or *Volvox* in other words is a permanent morphological equivalent of the blastula stage in the ovum of a Metazoon, and a spermatocyst holds a similar relation to the encysted reproductive stage at the terminus of life in an Amœba. It, however, occurs at the beginning of life in this specialized male cell among Metazoa. The spermatozoa also, which are produced by fission of the nucleus, resemble the young of the Amœbinæ and many other Protozoa in form, but have, through earlier inheritance of characteristics, acquired the functional power of the adult male Protozoon, and are therefore, as compared with Protozoa, to be estimated morphologically and functionally as microgonids with highly concentrated development. In no other way can we account for the premature exhibition of power shown by these forms in seeking out the egg and forcing their way into the vitellus. Ultimate union with the female nucleus of the ovum by passage through the vitellus is quite distinct. It has appeared to us to be, like concrescence in low forms, an exhibition of mutual attraction which indicates affinity, and, like all sexual processes, a vital attraction of greater intensity than mere fusion by growth, and in no way attributable to accident. The habit may have sprung from the habit of concrescence, just as we can only imagine all sexual processes as springing originally from concrescence through its transformation into a habit preparatory to reproduction by division, as among Myxomycetes. Cienkowski considers concrescence to have originated from the habit of feeding, and the results of concrescence, reproduction by fission, as a function due to the same causes and having the same results as assimilation (Archiv mikr. Anat. vol. ix.).

There is a gradation in the stages of development of the ectoderm, endoderm, and mesenchyme in the sponges which shows they have retained the ancestral protozoonal characteristics in some cells more than in others. Thus the ectodermic cells in all the Porifera become permanently transformed into flat epithelial cells, losing their feeding-organs, the collars, and flagella; whereas the cells of the endoderm in some forms, such as the Ascones, probably never lose these organs at all, and in others lose them only transiently at certain stages, or

* For results of protection in producing concentration of development see "Genesis of *Planorbis* at Steinheim," Mem. Bost. Soc. Nat. Hist. I. Anniv. 1830-1880; Fossil Ceph., Mus. Comp. Zool., Proc. Amer. Assoc. Adv. Sci. vol. xxxii. p. 32; also Balfour's Comp. Embryol.

only locally on the walls of the archenteron in the intervals between the diverticula (primitive ampullæ) *.

In the mesenchyme of sponges the cells have been subjected to fewer changes, and they preserve their ancient amœboidal forms unaltered. The comparatively great change in the evolution of the group probably took place after the transfer of the principal seat of assimilation from the endoderm to the mesenchyme. This transfer possibly occurred during the genesis of Sycones and other higher forms.

The researches of Saville Kent among Protozoa have shown that the collar and flagellum are feeding-organs, and we must imagine them as having a similar meaning in the internal cavity of Ascones, the lowest forms of sponges.

When we consider the whole series of transformations of the ovum it becomes apparent that it is at first an autotemnon having the Amœba stage well and clearly developed. The ovum develops parallel with the spermatocyst through the period of division of the nucleus into two parts, the masculonucleus and the feminonucleus. We have tried, in common with some other authors, to show that the masculonucleus is probably thrown off in the polar globules during a process of agamic division of the nucleus, and that these are the homologues of the masculonuclei excluded from the spermatocyst after having been transformed into spermatozoa.

The remarkable essays of Professor Ed. Van Beneden on the bisexual nature of the nucleus are the only embryological writings which produce the proofs of this hypothesis in illustrated form. This author ("Fecond. Maturat. de l'Œuf," Archiv. de Biol. tom. vi. 1883) advances precisely similar views to those of Dr. Minot, and shows the phenomena of fecundation and the double composition of the maritonucleus in a series of remarkably clear illustrations. Van Beneden claims to be the discoverer of the bisexual composition of the nucleus of the ovum, and refers to his paper of December 1875 (Bull. Acad. de Belg. vol. xl. 1875) as containing the first statement of his discovery. Though not pretending to forestall the judgment of those better qualified to decide the merits of these claims, we find that Professor Van Beneden was the first to announce the basal facts of the bisexual theory, but that he did not give all of the essential conditions of the phenomena of conjugation between the male and female parts of the nuclei in his first

* Von Lendenfeld (Austral. Sponges, Proc. Linn. Soc. N. S. Wales, vol. ix. pl. iv.) describes *Homoderma sycandra* as having these cells equally distributed all over the endoderm as well as in the single ampullæ.

paper. This author, in the work just cited (p. 700), suggests that the peripheral pronucleus is probably partially formed of spermatic substance, that the central pronucleus is female, and that the segmentation-nucleus is a compound body resulting from the union of these two, and is therefore probably bisexual. This statement includes all the basal facts of the genoblastic theory, with, however, two important exceptions. It omits any notice of complementary behaviour or functions of the useless parts of nuclei in both the spermatocyst and ovum. This essential condition of the conjugation of the nuclei does not seem to have been elaborated by Van Beneden until 1883, long after the appearance of Dr. Minot's paper. Dr. Minot (Proc. Bost. Nat. Hist. vol. xix. p. 170) proposed to name the original bisexual nucleus "genoblast," the female part "arsenoblast," and the male "thelyblast," and these terms have precedence of those we have advanced, or of those proposed by Van Beneden; but we have preferred to use names which retain the word nucleus, as more expressive of the true relations of derivative nuclei.

If this is true the occurrence of this process of excluding the masculonuclei in the ovum during the agamic stage exhibits an earlier inheritance of a characteristic which in the Protozoa occurs only after and as a result of impregnation, except possibly in some of the more specialized Flagellata and Ciliata, where the existence of spermatocysts and spermatozoids leads one to anticipate a corresponding differentiation. The female zoön certainly appears to be in reality an ovum, and to develop like one into a blastula, as pointed out by Bütschli.

This view includes some results worthy of attention. The concrescence of Protozoons, as in cases cited by Drysdale and Dallinger, and in some plants where the whole contents of one pair of cells or more than one pair of cells are mingled together, is asexual conjugation, but not sexual conjugation. The latter occurs only by the exchange of differentiated parts of nuclei, or between the larva-like spermatozoa and the complementary part of the nucleus in the ovum. Thus such forms as *Eudorina* and *Volvox* might be called, on account of their morphology, Blastrea, and could, because of their mode of reproduction and the existence of but one layer in the body-wall, be appropriately designated as true Mesozoa.

With regard to the meaning of the early stages of the ovum we come nearer to Bütschli (Morph. Jahrb. 1884) than any other author, and regard his placula theory as opening a way far more promising than any so far proposed. This author, however, voluntarily rejected the aid of the sponges in his arguments, under the erroneous impression that they were

Protozoa, and holds an essentially distinct idea of what the placula is. The embryo of the Calcispongian is, according to our opinion, a single-layered placula or a monoplacula, and directly comparable with the undifferentiated flat colonies of Protozoa which are more primitive than the blastula form, and represent the simplest condition of an autotemnic colony of Protozoa, like *Desmarella* of Saville Kent, though not possessed of cilia at this stage, and therefore more nearly perhaps representing a mass of amœboid forms.

The formation of the apical or esoteric cells of the upper layer from the cells of the monoplacula transforms this stage into a diploplacula, the older or basal cells becoming our exoteric cells. True ectoblastic and endoblastic cells first appeared during the gastrula stage, and are supposed to be identical with the differentiated cells often found in the blastula and placula. But in both of these last they are in distinct association and correlate with distinct forms, and should be considered as simply exoteric and esoteric cells. They are not true ecto- or endoblasts until they assume the relations of an external and internal layer, as in the gastrula stage. The absence of the placula in many forms may be explained as due to concentration of development. The protected conditions under which the ovum originates make the constant retention of the placula unnecessary, and favour the earlier inheritance of the morula or mulberry stage; in fact any quickening of the processes of growth would bring about this change, and the morula stage is only a heaping up of cells into a more massive colonial growth. The rounded globular forms of the morula would thus replace the placula earlier in the life of the embryo, and occasion its disappearance in more highly specialized forms, as in the Carneospongia.

This theory is apparently very similar to that of Bütschli so far as relates to the origin of the placula, but differs in making the morula an important stage of the evolution of forms, and in insisting upon the placula as primitively monoplaculate and only secondarily diploplaculate. Bütschli's placula is in reality a later stage, a specialized flattened stage of an embryo Metazoon.

Bütschli points out the resemblances of the embryo of *Cucullanus*, *Rhabdonema*, and *Lumbricus* to the placula, and the apparently primitive mode of forming the segmentation-cavity in the latter by the separation of the two layers is also given in detail by him. Bütschli also considers the *Trichoplax adhærens* of Schultze as a living illustration of a full-grown, primitive, placulate form.

We ought to find primitive stages in the embryos of a primitive type, and this is eminently the case with Porifera. We should anticipate the opposite with a higher type like the worms or any metameric animal, and this appears to be borne out by what Bütschli brings forward in support of his theory.

In *Cucullanus* the earliest stages are rounded, and we cannot agree with Bütschli that the flattened form which follows this is a primitive placula or diploplacula. The primitive placula is a single layer which becomes double or diploplaculate, and in both stages must precede the morula, and cannot succeed this stage. It will be seen by our remarks above that the esoteric and exoteric differentiations would have occurred normally before the morula stage in the placula of *Cucullanus* or else in fusion with it, and therefore the double-layered placula of Bütschli would be necessarily a flattened morula in which the two layers had already been formed. The relations of the planula stage in *Cucullanus* and *Lumbricus* to the gastrula also indicate that it is simply a modification of the morula stage, and not comparable with the earlier premorula stages of the embryo. The formation of the gastrula in *Cucullanus* is a beautiful example of extra growth of the ectoblast, as has been pointed out by Balfour; and in this and in *Lumbricus* a true embolic gastrula is formed by this process, which is not more primitive than that which occurs in the *Ctenophoræ* or *Tubulariæ*. The gastrula, in other words, is formed according to a highly concentrated secondary mode of development, and not by primitive or simple processes. We should therefore, even while adopting Bütschli's theory, decline to accept his typical examples as true illustrations of the theory, and hold rigidly to the law of succession in the stages of the embryo for justification of this position.

We cannot give a better illustration of what we mean by a monoplaculate embryo than Hatschek's *Amphioxus* in the four-celled stage *, nor of our diploplacula than the same in the eight-celled stage, when the cells of the esoteric layer are first differentiated, which occurs even before the two poles of the embryo become closed and long previous to the stage when the blastula is formed.

Immediately after the diploplaculate stage the ovum of Porifera and *Amphioxus*, as well as some other types, presents a stage during which it is a tube open at both ends. The hereditary significance of this stage indicates a tubular ancestral form, through which water would freely circulate; and

* Arbeit. d. Zool. Inst. d. Univ. Wien, iv. Heft i. pl. i.

this strengthens our position with regard to the meaning of the aula of the blastula.

The central cavity of the blastula stage, the so-called Protogaster of Häckel, connects with the exterior by a blastulapore, the "Protostoma" of Häckel, which is normally closed later in the growth, but remains open for long periods in some sponges, as may be observed in the figures of *Sycandra raphanus* and in the larvæ of siliceous sponges, as in the embryos of *Halichondria* and *Tethya*. The assumption that such a primitive cavity necessarily originated as a gastric cavity seems improbable.

The prototype of this cavity, the aula, must have first appeared as a central hollow in a moving colonial form of Protozoa, simply as a mechanical necessity of the habits and mode of growth, and might have been useful as a float; but was probably not a gastric cavity, but, on the contrary, similar in every way to the internal cavity of the *Volvox* blastula. The additional advantage of the possession of such a hollow in enabling the cells to use both sides instead of one, and to perform the functions of respiration, ingestion, and excretion more completely, is obvious. The growing of the cells of the ovum into a hollow sphere, the blastula with its blastulapore opening externally, is described by Bütschli as essentially similar to the growth of the adult floating spherical colonies of *Volvox* and *Eudorina* from a single zoön by fission. This author (Bronn's 'Thierreich,' Protozoa, pl. xlv.) gives a series of figures illustrating the development of the asexual zoöns of *Volvox* which fully substantiate his comparisons, and, together with Carter's, show that the closest comparisons may be made between the early stages of the ovum and those of all forms of *Volvox*, which is an open blastula like that of some Porifera before it leaves the parent colony and becomes free.

All of these comparisons seem to be much opposed to Bütschli's supposition that the primitive cavity of the blastula originated from a separation of two layers rather than as a stage of development from one primitive layer and the formation of an aula.

In order to account for the differentiation of the esoteric cells we have imagined them as necessarily by position feeding-cells in the ancestors of the diploplaculate stage. In the free morula and closed blastula the same cells or their more modified descendants would tend to retain similar functions. The differentiation of the poles would occur in this blastula form according to the same law as is observed in the higher animals, and the tendency already initiated of the zoöns of one pole to become exclusively feeding-zoöns would be increased by more frequent contact with food and by being constantly occupied in the act of ingestion. The differentiation of the cells having been thus established and kept up by a continuance of similar habits, and the aula correlatively developed, we should have a free moving form with the cells at one pole feeding-cells, and at the other probably more efficient as respiratory cells. These last need not be necessarily inefficient as feeding-zoöns, but might have remained quite capable of this office as well also as that of developing flagella for moving the body, and, in fact, resembling in aspect and structure what we actually find in the amphiblastula of some sponges. We here claim for the exoteric or ectoblast cells that their possession of collars and flagella implies the existence of powers of ingestion. We think the negative evidence adduced by Metschnikoff and others with regard to these cells in the embryos of sponges is entirely inadequate to prove anything except the fact that they have not seen them actually feeding, and does not weigh against the observed functions of the collars and flagella of the Flagellata, especially the positive and convincing proofs brought forward by Saville Kent.

The parenchymula is a recently discovered stage of the embryo immediately succeeding the closed blastula. The esoteric cells differentiated during preceding stages have been found by several authors to quit the exterior, where they originated, and wander into the interior, where they presumably give rise to the endoblastic cells subsequently found there.

A differentiated colony, like the amphiblastula, with the cells at one end becoming better fitted to take in food, could be transformed into a parenchymula by the migration of differentiated feeding-cells into the interior, and the parenchymula could thus have been transformed into a true gastrula. There are no living forms, so far as we know, with which the parenchymula can be compared, and its probable meaning has already been indicated by other writers, especially by Metschnikoff, namely, that it implies a radical form in which the mesenchyme has arisen as a primitive mass by delamination.

The inwandering of the esoteric cells of the parenchymula might be reasonably assumed as in part due to pressure. This appears to be a primitive mode of forming the endoderm as stated by Schmidt and Metschnikoff, and therefore we should have to consider pressure as simply a possible cause aiding the tendency to inwandering, as it appears in the habits of these cells of the parenchymula. It is possible that this tendency was derived from ancestors in which a primitive invagination appeared as a later characteristic of the development, due to excess of growth in peripheral parts, and that the same conditions of growth and pressure would continue to be present in the similar parts of the young of descendent forms as long as the surroundings and habits were sufficiently similar and did not interfere with hereditary tendencies. Thus we should have to regard the habit of inwandering of the esoteric cells as giving rise to the primitive endoblast, and this last as a permanent stage preceding the transient gastrula due to invagination. The continued action of the same cause as gave rise to the tendency to inwandering, namely the pressure occasioned by the rapid multiplication of external cells by growth, and the action of heredity, would secure this result.

The fact that the esoteric hemisphere is an excessive peripheral outgrowth of cells in the amphiblastula is in perfect accord with the successive stages in the development of pits and minor invaginations of the ectoderm. These are universally in their primitive stages peripheral outgrowths of the outer membranes, which form primitive hollows, and then these cups become hereditary invaginations in the embryos of descendent forms. The formation of stomodea and other ectodermic invaginations can thus be accounted for as in every way parallel to formation of the gastrula and due to similar causes.

The invagination of the endoblast in the ordinary form of the gastrula is immediately accompanied and caused, according to Whitman, by pressure arising from the unequal growth of the hemispheres. The pressure on the endoblast after invagination is shown by the forms of the cells, which become elongated along the middle part of the cup, as in the well-known case of *Amphioxus* described by Kowalevsky and many examples by other authors. The growth and excess of pressure is also evinced in the elongation of the planula and the tendency of the at first broad blastopore to close up to a narrow opening by growth of the ectoblast. The usually columnar aspect of the ectoblastic cells of the planula, their longest axes being radial or at right angles to the direction of the pressure, is also favourable to this theory. These cells may be attenuated in Porifera at this stage (Barrois, Époug. de la Manche), so as to assume an almost linear aspect under low powers of the microscope. We feel obliged to join those authors who regard the planula-stage as an abbreviated form of the gastrula possibly directly derived from the epibolic gastrula. The succession of the stages is first a peripheral outgrowth, increasing continually the diameter of the amphiblastula, then invagination, then peripheral growth of the ectoblast, followed by elongation of the planula and contraction or obliteration of the blastopore. Heredity in these cases seems to be subordinate to growth; but this we think is due to the necessarily identical action of these inseparable forces. Heredity and growth are also necessary in order to account for cases of epibolic gastrulæ as well as for the existence of the planula. The action of heredity in the planula is obvious; but in the transitional epibolic gastrula the obvious mechanical action of growth still interferes with the clear perception of the influence of heredity. The growth of the ectoblast cells is so rapid in the last named that the endoblast cells become enclosed, as in the Ctenophoræ, and the gastrula is formed by a process much shorter than is usual in embryos of the embolic type.

In a planula we can see very clearly that some other force in addition to growth has been at work, and that, whether we adopt Lankester's hypothesis or some other, we are equally obliged to call in the aid of heredity in order to explain the hidden steps by which the embolic gastrula has been transformed into this concentrated form of development through the epibolic gastrula as an intermediate stage.

Keller (Anat. und Entwickel. einiger Spong. d. Mittelmeers, Basel, Georg, 1876) has given the fullest illustrated account of what we have, in common with Metschnikoff and Schultze, called the transient gastrula of the Calcispongiæ. A recent perusal of this interesting paper has suggested that there is probably no better field for the study of the effects of pressure upon cells than in these cases of transient invagination. It is possible that the invagination stage may be traceable directly to excess of growth in the ciliated cells and their subsequent evagination as outgrowths to the reversal of this process, and at any rate the field is a very promising one in this direction.

We have also noted in our original essay the probability that the medullary fold was primitively a stomodeal invagination due to extra growth, and we are able to quote in this connexion an observation of Dr. Hatschek's in addition to those of Kollmann and Gardiner.

Dr. Hatschek (Arb. Zool. Inst. Wien, vol. iv. 1881, pp. 45-48) attributes the origin of the primitive segments and other changes of form in the embryo of *Amphioxus* to the growth and energy of cells. He explains the origin of the medullary plate by differentiations in the cells caused by the extra growth of the neighbouring cells of the ectoderm, and attributes the rise of the ends and final enclosure of the neural canal to lateral outgrowths due to the same cause *.

The general presence of the different forms of the gastrula, including the planula, indicates, as we have tried to show above, that Häckel was right in supposing that these stages indicated common ancestors for the whole animal kingdom. To this we have also joined the architroch of Lankester, imagining in common with this author a very ancient origin for the circles of cilia around the blastopore of the primitive gastrula-like ancestors of the Invertebrata.

The history of the structural transitions through which the layers of the body pass in their subsequent history sustains the view that the Porifera are the lowest type of Metazoa. The endoderm and ectoderm reach a highly differentiated stage and appear as flat epithelial membranes; but the middle layer remains a mesenchyme, containing, as stated by all authors, the reproductive bodies of both sexes. The appearance of spermatozoa and ova indifferently in the same animal shows that entire separation of the sexes does not take place so far as now known among the Porifera. It is not yet established that cross-fertilization occurs in any form, though there is as yet no ground for the positive assertion that it does not occur. The history of the early stages exhibits a larval form in which the interior is solid for a certain period and the mesenchyme plays a much more important rôle than in any other branch of the animal kingdom, as might be anticipated from the adult condition and importance of this layer in the morphology of the group.

We have also tried to show that the general morphology and development indicated the gradual evolution of series of forms from a type similar to Ascones, but without a skeleton, which we have considered directly comparable, as stated by Häckel, with the gastrula. During this evolution the mesenchyme became more and more important, and as a result of its thickening the habit of budding was more or less suppressed, so that the higher types must be considered as individuals with a highly plastic form, liable to excessive outgrowths, but not as branching Metazoons. The archenteron also remains persistent throughout life, gives rise to simple diverticula, or, in forms with thick mesenchyme, diverticula themselves form branching tubes.

The fact that no internal column or body-cavity is formed,

* See also His, 'Unsere Körperform,' 1875, pp. 60, 61, 83, and 178, who has essentially the same idea of the relations of growth of cells and development of organs.

in spite of the opportunity offered by the increasing thickness of the mesenchyme, is very significant. It is not yet established that the mesenchyme does receive some additions in course of its growth from the endoderm and ectoderm, but, so far as the histology is now understood, it is doubtful.

In other words the Porifera are intermediate with regard to structural composition between primitive larval individuals, like the free larvæ of all colonial types, and the differentiated colonies which arise from such primitive individuals after they become attached, as in the Hydrozoa. They contain all the elements necessary for the formation of complicated colonies; but in consequence of the less differentiation of the mesenchyme their primitive individuality is maintained and the processes of budding take place internally and externally without perfect correlation. That is, the exterior has outgrowths and so has the archenteron, but these are not strictly coincident and produce true buds only in forms with thin mesenchyme.

The evidence in favour of the opinion that the diverticula or ampullæ are strictly homologous with the archenteric diverticula of all other animals is very strong. The young have no diverticula until the ampullinula is formed, and this correlates with the absence of these organs in the adults of the lowest type, Ascones. These facts among sponges seem to be in accord with the history and development of the diverticula among Hydrozoa and Actinozoa, and lead to the conclusion that in all of these three types the diverticula are homoplastic organs, and not found in the lowest forms of these groups or in the early stages of development of the normal forms.

The considerations we have presented above have therefore a direct application to the results of the work done of late years by Semper, Dohrn, and others in tracing the origin of the Vertebrata to some worm-like type. The whole of this evidence hangs necessarily upon the probability that the somites of the embryo of *Amphioxus* imply descent from a segmented animal; whereas, if we are correct, exactly the opposite view may be considered as the more probable; and the very close comparisons made by Semper between what he considers homogenous organs and parts in Vertebrata and Vermes can only be considered as evidence of the production of homoplastic effects by means of similar modes of growth and the similar habits of elongated and necessarily bilateral animals.

We have objected to the theory that the Vertebrata may be considered as descended from a Cœlenterate ancestor, because the actinostome probably arose independently and very late in the phylogenetic history of the Hydrozoa, and undoubtedly arose independently in the Porifera. A stomodeum as it appears in the ascula stage or in a sycon or ascon may be a single opening not due to invagination, merely an enlarged pore or outlet. The cloaca of the more specialized sponges is first an outgrowth of the peripheral parts which becomes inheritable and causes the appearance of the ectoderm as a lining layer extending to an indefinite depth into the interior. A stomodeum, also, does not exist in most of the Hydrozoa except in the primitive shape of an outgrowth, the hypostome, which is the homologue of the internal actinostome of the Actinozoa. These facts and the late stage at which it arises (in the Actinozoa during the gulinula stage) show us that, so far as these types are concerned, it is an independent and homoplastic organ in all of them.

There are no exact comparisons between the embryos of Ascidia and *Amphioxus* and those of the Invertebrata which seem to include any stages later than the planula. Those that have been traced between the mesoblastic somites indicate homoplastic organs, and seem to have no phylogenetic meaning so far as the whole of the Vertebrata are concerned. The distinct modes of development of the anterior invaginations of the Vertebrata show that they had a different origin from the anterior tube of the actinostome, and cannot be considered homogenous with that organ in the Cœlenterata. The medullary invagination is at first a stomodeum arising as a funnel around the blastopore, and then spreads forward in the shape of two folds, which subsequently form a tube, and it is probable that the notochordal tube and the lateral differentiations of the archenteron may have had a similar homoplastic simplicity of structure.

The development in Ascidia of the notochordal cells and muscle-cells from the walls of the archenteron invites the suggestion that no true diverticula exist in this type. That the lateral muscles might have arisen as entirely disconnected and more primitive structural elements than the cœlomata is shown by Kowalevsky's work on *Cassiopea* already quoted (Soc. Friends of Nat. Hist. &c. Moscow, pl. ii. figs. 10–13). In this Hydrozoon portions of the archenteric walls grow out and become directly converted into muscles, but no cœlom is formed.

The notochord may have primitively originated as a tube, but connexion with the hypophysis seems to be a necessary condition of this theory; and though this is highly probable, it is not proven. The homoplastic origin of the notochord, when explained in this way, agrees with the subsequent origin of segmentation in the vertebræ, as suggested by Cope. These facts and agreements in theory render it highly probable that the whole phenomena of segmentation as shown in the distribution of the muscles themselves, the appendages, and internal organs, including even the primitive somites, may have arisen independently in the Vertebrata in response to the simple mechanical requirements of motion in elongated bodies. Herbert Spencer, in a treatise much neglected by naturalists (Princ. Biol., Amer. ed. 1871, vol. ii. p. 199), has clearly shown that the origin of the notochord and of segmentation of the vertebræ and muscles may be attributed to muscular strains, and our speculations, though entirely independent, cannot lay claim to any original merit.

Our results are similar to those of Häckel so far as they distinctly point to the gastrula and planula as the earliest stages which have a general genetic meaning for the Metazoa, and show that these indicate a stock-form for the whole of the Metazoa. The clear distinctions between the type-larval stages in different branches of the animal kingdom and the fact that the type-larval stages make their appearance invariably after the planula or gastrula, and never, under any conditions, break this natural succession, give strong support to this opinion.

It is possibly premature to say that no one type can be claimed to have descended from any other; but the Porifera, Hydrozoa, Actinozoa, and Vertebrata appear to us entirely independent of each other. It is also very suggestive that two so closely allied groups as the Actinozoa and Hydrozoa can be considered as homoplastic types, and that many examples have been brought forward by the author and Professor Cope * among Cephalopoda and Vertebrata, where smaller and more closely allied groups, orders, families, and genera show the same phenomena, and are plainly homoplastic with reference to the origin of many important characteristics of structure. These results sustain the opinion that homogenous characteristics are frequently so similar to purely homoplastic characteristics that it is not safe to consider any characteristics occurring in distinct groups as homogenous until their phylogenesis has been traced or their comparative embryology is fully understood.

The hypothesis of the common but independent origin of types is also supported by all collateral evidences. The results of palæontologic research have carried back the origin of

* Cope, who first pointed out these relations in the same sense as Lankester, used the terms "homologous" for homoplastic and "heterologous" for homogenous.

distinct types further and further every year. It is now established that there was an excessively sudden appearance of vast numbers of forms in the Cambrian, or perhaps earlier, as claimed by Professor Marcou and others.

We have applied this specific statement as a generalization to the history of smaller groups of fossils in several branches of the animal kingdom and in many formations, and have found that the sudden appearance of the smaller groups occurs according to the same law.

There is an obvious plasticity in the animals which first make their appearance in any unoccupied field, or at the beginning of any new formation, which reminds one of the plastic nature of the most generalized type of Metazoa, the existing Porifera. The generalized types, which always occur first in time, exhibit like sponges exceptional capacity for adaptation to the most varied requirements of the surroundings and all of the conditions of the new period or habitat by the rapid development of numbers of suitable and more highly specialized forms, species and genera.

The whole picture as presented by morphology, embryology, and palæontology favours the hypothesis we have previously advanced in other papers, namely that the early geologic history of animal life, like the early stages of development in the embryo, was a more highly concentrated and accelerated process in evolution than that which occurred at any subsequent period of the earth's history.

The history of the Porifera and higher Protozoa suggests also that the evolution of the Metazoa may have occurred more rapidly than we can now calculate. One of the great errors of the present day is the assumption that such changes and transitions occurred slowly and gradually; and it is evident that this assumption is based almost wholly upon investigation of the more highly specialized animals, in which the capacity for change may be reasonably considered as very much less than in their more generalized and embryonic ancestral forms.

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## XXIII.—*Preliminary Communication on some Investigations upon the Histological Structure of the Central Nervous System in the Ascidia and in* Myxine glutinosa. By Fridtjof Nansen *.

It is proposed in the following pages to give only a mere

* Translated by W. S. Dallas, F.L.S., from the 'Bergens Museums Aarsberetning for 1885,' pp. 55–78.